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FLUCTUATIONS IN CALIFORNIA QUAIL**

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Made in United States of America
Reprinted from THE JOURNAL OF WILDLIFE MANAGEMENT
Vol. 34, No. 2, April 1970
pp. 249-260

THE INFLUENCE OF WEATHER ON POPULATION FLUCTUATIONS IN CALIFORNIA QUAIL

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Abstract: Age ratios of quail (*Lophortyx californicus*) in San Luis Obispo County, California, were available for 14 consecutive years. Ratios were based on hunter-shot samples averaging 672 birds per year. Weather data were compiled and a multiple linear regression of quail productivity on selected weather parameters revealed a close relationship ($P < 0.01$). Quail productivity seemed to be a function, in order of importance, of (1) soil moisture in late April calculated from temperature and rainfall data, (2) proportion of breeding females over 1 year old, and (3) the seasonal rainfall from September to April.

Three geographically isolated wild quail populations and one penned population were observed during two breeding seasons that were very different in productivity. In 1963, quail produced many young. The breeding period was characterized by intense activity and persistence of breeding effort extending, in captive birds, to production of second broods. Vegetation that year included many annual forbs growing vigorously during the breeding season. In 1964, production of quail was very low on all areas. The birds seemed to lack reproductive drive, and breeding effort terminated early. Early vegetation that year was sparse.

Reproductive success and the resultant population levels of California quail are known to vary considerably from year to year. As far back as 1887, quail were observed to remain in coveys and to fail to breed in unfavorable years (Grinnell et al. 1918; Sumner 1935). Storer et al. (1942), Ralitt and Genelly (1964), and McMillan (1964) have reported large annual variations in the proportion of juvenile birds in California quail populations in the fall. Among California quail introduced into New Zealand, the ratio of juvenile to adult birds was found by Williams (1963:444) to vary from 0.17 to 1.15:1 over a 14-year period.

In the reports cited the variation in production of young is frequently attributed

to weather, sometimes directly, but more often indirectly through its influence on the vegetation. The description of the weather is often in such general terms as "a dry winter," "spring wetter than usual," etc., but sometimes more specific, as "October to March rainfall."

The present study was undertaken: to investigate the particular weather factors relating to reproductive success; to determine the joint effect of such weather factors on biological parameters affecting population levels; and to find combinations of weather factors which would be significant in predicting quail production.

Several departments of the University of California provided facilities and assistance: the Animal Behavior Laboratory, the Survey Research Center, the Public Health Computer Laboratory, the Department of

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Table 1. Distribution of quail by sex and age in fall hunting samples, Shandon area.

YEAR	ADULT MALES	IMMATURE MALES	ADULT FEMALES	IMMATURE FEMALES	IMMATURE ADULT RATIO	TOTAL NUMBER
1949	80	164	59	175	2.32	481
1950	65	127	52	140	2.20	374
1951	178	10	180	13	0.08	387
1952	87	363	80	377	4.30	915
1953	170	94	149	90	0.57	509
1954	140	333	80	339	3.00	898
1955	185	302	130	309	1.90	932
1956	151	203	80	198	1.70	638
1957	149	214	131	207	1.50	701
1958	157	311	80	272	2.40	820
1959	205	80	145	71	0.45	507
1960	110	157	91	161	1.54	525
1961	192	119	152	103	0.65	568
1962	193	431	131	410	2.00	1173
1963	250	292	161	264	1.35	967
1964	167	0	129	5	0.04	307

Data from McMillan (1964, and personal communications).

Entomology and Parasitology, and the Museum of Vertebrate Zoology. I am indebted to I. McMillan for permission to work on his ranch and for other assistance, to J. Davis and K. White for assistance and facilities at Hastings Reservation, to Catherine Pyle for assistance in maintaining quail in the enclosure, to W. F. Taylor for guidance in statistical analysis, and to G. M. Christman for assistance with graphs. A. S. Leopold gave advice and assistance throughout the study and constructively criticized the manuscript. R. F. Labisky also read the manuscript and offered suggestions.

METHODS AND MATERIALS

Study Areas

Quail populations were studied in three principal areas in California. These will be referred to as *Berkeley* in Contra Costa and Alameda Counties; the *Hastings Reservation* in Monterey County; and *Shandon* in San Luis Obispo County, especially on the McMillan Ranch. Some additional observations were made in Kern and Monterey Counties.

Population Records

Data on sex and age ratios in quail populations for previous years were available for all three areas (Halt and Genelly 1964; McMillan, 1964; and original banding records at Hastings Reservation.) The length of record and size of samples at both Berkeley and Hastings Reservation were too small to permit adequate statistical analysis, and correlations are reported only for Shandon data. Field observations in all areas are included in the discussion. Table 1 shows data on quail sex and age-classes in fall hunting samples taken at Shandon and reported by McMillan (1964: 705), supplemented by his unpublished field notes.

Weather Station Records

Temperature and rainfall data for Paso Robles (USWB Station 6730), 15 miles west of Shandon, were made available on punched cards by the National Weather Records Center, Asheville, North Carolina. Rainfall data for Cholame (USWB Station 1743), 8 miles east of Shandon, were ex-

tracted from U.S. Weather Bureau climatological publications; no temperature data for Cholame were available. Additional data were obtained from the hourly weather observations of the F.A.A. station at the Paso Robles Airport for the period February, 1963 to May, 1964.

Weather instruments were installed to record temperature, humidity, and rainfall data within the quail habitats in the three study areas during the 2 years of field study. A comparison of the data from the Shandon installation with official data from Paso Robles and Cholame showed the day-to-day variations to be similar and indicated that the official data could be accepted as indicating weather variations in the Shandon quail areas.

The volume of data in these records—maximum and minimum temperature and amount of precipitation for each day—required some reduction. Means of weather elements were calculated for 10-day periods (referred to hereafter as "decades") numbered consecutively beginning with September 2 of each year. Previous studies have found periods of this order to be desirable (Nice 1937, Allison 1962, Errington 1942). The days remaining after 36 decades were ignored.

Captive Quail

In early March, 1963, four male and four female wild quail (half adults and half yearlings) were trapped, marked with colored leg bands, and placed in a 100- × 100-ft enclosure on the Animal Behavior Station, Berkeley campus (Francis 1965:541). One female was killed by collision with the fence on April 19, leaving a breeding population of three pairs and one extra male.

On February 24, 1964, I reduced the population to four pairs by trapping and releasing excess birds. The remaining birds were one pair over 2 years old, one pair in

the second breeding season, and two pairs of yearlings hatched in the enclosure the previous year.

An observation hut built into one side of the enclosure allowed close observation of the birds with a minimum of disturbance. I observed behavior and breeding phenology throughout two breeding seasons. Supplementary food (poultry chow) and water were supplied.

Trapping

Trapping programs were carried out to obtain sex and age ratios in the quail populations, and to estimate population size, in the Berkeley Hills, at Hastings Reservation, and at the McMillan Ranch in the Shandon area. Wire mesh, funnel-type traps were used at all locations.

Field Observations

Observations during 1963 and 1964 included amount and species composition of vegetation, breeding behavior of quail, breeding phenology of both captive and wild quail, and examination of 22 specimens. Observed ratios of young to adult quail were very different during these 2 years; 1963 was a year of good production, while production in 1964 was almost a complete failure.

RESULTS

Vegetation

Quail enclosure.—In 1963, a variety of forbs were present in abundance, the more prominent species in the spring including *Erodium cicutarium*, *Medicago apiculata*, *Medicago hispida*, *Geranium dissectum*, *Anagallis arvensis*, *Viola sativa*, *Brassica campestris*, and *Ranunculus californicus*. Grasses, thistles, and other Compositae were also present (Plant names follow Jepson 1960).

Medicago and *Erodium* are among im-

portant natural foods for quail (Sumner 1935:172-173) and presumably are highly nutritious; green leaves of *Vicia* were also extensively used by the quail in the enclosure.

In 1964, forbs decreased greatly and grasses increased, in comparison with the previous year. None of the spring-blooming forbs were present, but thistles increased noticeably. Observations of feeding birds showed a greater use of grain supplements, compared to natural foods, than in 1963.

Hastings Reservation.—A heavy growth of grasses in the open meadows in 1963 remained in 1964, although with little new growth. *Erodium cicutarium* was common in both years, but other forbs were less numerous in 1964 than in 1963.

Shandon.—At McMillan's Ranch, growth of vegetation was exceptionally good in 1963. Interspersed with pasture grasses were abundant forbs of several species of *Eriogonum* and *Lupinus*, *Medicago hispida*, *Amsinckia douglasiana* and widespread and abundant *E. cicutarium*. These are all quail food (Sumner 1935; Glading et al. 1940), and probably important sources of essential nutrients. Poorer growth was evident in 1964, and the forbs found the preceding year were scarce or absent. Close examination of a pasture in which quail were observed feeding showed many very small *Erodium* plants, and the quail in this area showed no signs of malnutrition in the quantitative sense.

Breeding Behavior

Berkeley quail enclosure.—Observations were made for a total of 60 hours on 58 days from March 14 to June 19, 1963. Normal pairing may have been disrupted by trapping, but three pairs formed by April 28. Little aggressive behavior was noted among the birds in the enclosure, but the males reacted to "squill" calls (Sumner

1935:200-205) from wild birds outside by running along the fence, looking out, and answering. The wild birds seemed to be strongly attracted to those in the enclosure, and in many cases would follow a feeding pair or group by walking across the top of the enclosure. "Cow" calls were frequent among the wild birds, and were occasionally answered by males in the enclosure. Copulation by the captive birds was observed on nine occasions.

In 1964, observations were made for a total of 23 hours on 34 days from March 2 to June 13. Pair formation was first noted on March 8. No aggressive behavior was observed among the eight captive birds; there was little calling of any kind either in the enclosure or from birds outside, and copulation was not observed at any time. The birds fed frequently in a group rather than in separate pairs. An occasional male outside the enclosure approached the fence. On April 13, a male inside exchanged "squill" calls with a bird outside and seemed to attempt an attack through the fence. "Cow" and "squill" calls were heard outside the enclosure on about four occasions in May, but no "cow" calls were given by any bird inside. The birds were less active than during the previous year, spending more time resting in cover of the brush.

Hastings Reservation.—Pairing began in early March, 1963, and by the first part of May, the one covey observed had broken up completely into mated pairs and single birds. "Cow" calls were heard regularly. In 1964, in early March, there were no signs of pair formation in a covey of 25 birds; in April, however, most birds appeared to be paired, and a short cockfight, accompanied by "squill" calls was observed on one occasion. No "cow" calls were heard during the spring.

Shandon.—In early March, 1963, pair formation was well underway, with loose

pair-bonds evident in about one half of 500 birds seen; pairing was virtually complete by March 27. By May, at least 90 percent of the population, estimated at 1,500 birds, was distributed in pairs over the McMillan Ranch. "Cow" calls were heard frequently from late March through May; in one case, two birds kept up a steady exchange of calls lasting 15 minutes. Aggressive behavior, including chases, "squill" calls, and cockfights, was observed throughout the spring.

In 1964, pairing appeared to reach about the same stage in early March as it did in 1963, with loose pair-bonds evident in about half of 465 birds seen. In April, however, most of the 500 observed quail were still in loosely associated groups, with many birds remaining in pairs within the group while feeding. About one fourth of the birds showed no signs of being paired. By early June, the five principal coveys had reformed, with only 6 to 7 percent of the birds remaining paired. The only chicks seen during the entire season were a group of 11 accompanying two pairs of adults, and a single chick with an adult male. The other birds seemed to have abandoned all nesting attempts; 57 adults trapped on June 8-9, 1964, were all molting, and had no young birds with them. Aggressive behavior was observed only in April, when I observed one cockfight, with accompanying "squill" calls, and two chases; no "cow" calls were heard at any time during the spring of 1964. The general impression, except for the pairing of birds in March, was that of absence of reproductive activities; by June, the behavior was that of fall coveys in a sexually inactive state.

In summary, the behavior of quail during the breeding season showed that initial pair formation took place in about the same way and at the same time in the 2 years. In the productive year of 1963, however,

Table 2. Ratio of immature to adult quail in trapping samples (T), direct counts (C), and hunters' bags (H) by locality, 1963 and 1964.

LOCALITY	1963		1964	
	Ratio	Number	Ratio	Number
Berkeley	2.83 (T)	92	0.17 (T)	42
Hastings				
Reservation	3.38 (T)	35	0.71 (C)	53
Shandon Area	1.35 (H)	907	0.04 (H)	907
Hunter Liggett				
Military				
Reservation	3.08 (H)	653	0.64 (H)	479

the intensity of the pair bond increased as the season progressed, aggressiveness was high and remained so during the spring, and the "cow" calls typical of the breeding season were frequent. In 1964, the intensity of the pair bond decreased early in the season, and in the Shandon area the bond had dissolved entirely with the formation of coveys in May and early June. Little aggressive behavior was noted at any time, and no "cow" calls were heard except among wild birds in Berkeley. The difference in reproductive drive between the 2 years was evident in April, before nesting began.

Reproductive success

Reproductive success (production and survival of young) was measured by brood counts, by the proportion of young birds in trapped samples, and by the proportion of young birds in hunting bags. The differences were similar in all study areas; the ratios of immature to adult birds are given in Table 2. A brief summary of the observations in each area is given below.

Berkeley.—Ninety-two quail, almost the entire covey, were trapped, marked, and released in the fall of 1963 in the area adjacent to the quail enclosure; the ratio of juveniles to adults in this covey was 2.83:1. In 1964, fall trapping in the same area, plus birds trapped in the winter of

1964-65 by R. Jones and R. Fletcher, yielded 42 birds, with a juvenile:adult ratio of 0.17:1.

Among the captive quail, in 1963, two adult females hatched 33 eggs in their first nests, and one subadult female hatched none. Some of the chicks escaped from the enclosure when only a few days old; of the 15 remaining, nine grew to adult size, a survival rate of 60 percent. Second nests by both these females (each with a new mate) hatched a total of 19 chicks of which only four (21 percent) survived. The age ratio of these captive birds, after making corrections for those which escaped, was 3.14:1 compared to 2.83:1 in the wild covey trapped in the same area.

In 1964, with four pairs of quail in the enclosure, half adult and half yearling birds, five nests were located, containing a total of 74 eggs; five additional eggs were found on the ground, all but one close to one of the nests. Only two of these nests, containing 19 and 13 eggs, respectively, were incubated, both by the adult females, and all eggs but one hatched in each nest. Three abandoned nests contained 14 eggs each. The contents of one of these, plus three of the eggs found on the ground, were incubated artificially and 14 hatched; fertility was probably high in all clutches. Of the 30 eggs hatched by the adult females, only eight chicks were alive at the age of 2 weeks, and only three survived to adult size. The productivity for 1964 (allowing for the escape of one quail) was 0.59 young per captive adult, and 0.17 young per wild-trapped adult. The similarity suggests influences of the common environment.

The observations of captive quail show clearly that the failure of reproduction in 1964 was not attributable to clutch size or to fertility, which changed only slightly from 1963 to 1964.

Hastings Reservation.—In December,

1963, 35 birds, of a population estimated at 49, were trapped; the juvenile:adult ratio was 3.38:1. In August, 1964, close observation of a covey of 58 birds permitted an accurate age count. The juvenile:adult ratio was 0.71. Only six out of 17 adult pairs were accompanied by young, with an average of four young birds per successful pair.

Shandon.—On three occasions in the summer of 1963, I observed quail at close range from a blind near a water hole. Over 2,500 observations of individuals were recorded with an average of about four observations on each bird, and age estimated on the basis of size and plumage development. The average age ratio, combining young of all ages, was computed to be 3.28 young per adult. Hunting bags in the 1963 season totaled 967 birds, with a juvenile:adult ratio of 1.35:1.

In June and August, 1964, 12 young were observed among a population of 600 quail, a ratio of 0.02 juveniles per adult. Only 11 of 307 quail killed by hunters were young, a ratio of 0.04 young per adult. This represents the most complete failure of reproduction ever documented in this area, not excepting the 1951 case described by McMillan (1964:707).

On the Hunter Liggett Military Reservation in Monterey County, a ratio of 3.08 young per adult was found in a sample of 653 hunter-killed quail in 1963; among 479 quail checked in 1964, the ratio was only 0.61 young per adult.

Specimens

Five males collected in May, 1963, in the Shandon area and nearby Kern County all had fully developed testes (calculated volumes 266 to 496 mm³). Of four females collected at the same time, two had ovaries with developing eggs; one had completed laying, with regressed ovary; and one was

apparently not breeding, with an ovary weighing only 0.05 g.

In 1964, three males, collected June 8 on the McMillan Ranch, all had undeveloped testes (calculated volumes 18 to 35 mm³) and were molting, having dropped the 5th, 6th, and 7th primaries respectively. Of the three females collected at this time, one appeared to have a regressed ovary, the other two were undeveloped. They were also molting, having dropped the 5th, 6th, and 7th primaries respectively.

The livers of 14 specimens were frozen, and later analyzed for vitamin A content by a commercial laboratory. Mean vitamin A levels and standard errors for groups of specimens were as follows:

Shandon area, August, 1963: 4 birds—
132±62 IU/g.

Berkeley, September, 1963: 3 birds—
692±97 IU/g.

Hastings Reservation, Dec. 1963: 1 bird—
1331 IU/g.

Shandon area, June 1964: 6 birds—
793±140 IU/g.

Vitamin A levels in molting birds in the Shandon area in August, 1963, were low compared to the high levels in molting birds in Berkeley in September, both populations having produced approximately normal numbers of young. Vitamin A levels were also high in the birds from Shandon which were molting in June, 1964, following an apparent failure to breed.

ANALYSIS OF SEX AND AGE DATA

Data on the composition of quail populations shown in Table 1 were obtained from hunting bags. Although it has been generally accepted that such samples represent population sex, and age ratios, comparisons of hunting samples from different areas and at different times, and comparisons of trapping samples with hunting

samples in the same area were made. This was done to determine if such factors as differential susceptibility to hunting introduced any significant bias into the samples.

Significant differences were found in two cases. In one sub-area, the immature sex-ratio at the end of the hunting season differed significantly from the early-season sex ratio ($P < 0.05$) and also from the expected 1:1 ratio ($P < 0.01$). All other sub-samples showed immature sex-ratios very close to 1:1. In another sub-area, the adult sex-ratio at the end of the hunting season differed ($P < 0.05$) from that at the beginning of the hunting season, with fewer adult females in the late season.

Combining data for the two sexes, and looking at the age ratios only, I found no significant differences between areas, between early and late season hunting, or between hunting and trapping. The lack of a difference between hunting and trapping samples can mean only (1) that both methods of sampling give an unbiased estimate of the population composition, or (2) that both trapping and hunting are biased in the same way with respect to age groups. The latter hypothesis would be difficult to justify. Trapping of marked birds showed no consistent bias in frequency of capture of young versus old birds. The assumption is made, therefore, that the hunting samples give unbiased estimates of the proportion of young and old birds in the population sampled. There is more doubt as to how well the sex ratios are estimated.

Population Model

In order to make a quantitative evaluation of changes in sex and age ratios, a population model was constructed with the same observable parameters as the observed samples in the Shandon area (Table 1). If a population does not increase or decrease

Table 3. Numbers of California quail, by sex and age in a model population with a constant male survival rate and in proportions identical to those of hunting samples in the Shandon area for corresponding years.

YEAR	ADULT MALES	IMMATURE MALES	ADULT FEMALES	IMMATURE FEMALES	TOTAL
1949	153	362	140	343	1000
1950	219	428	175	438	1260
1951	274	25	277	29	596
1952	127	573	125	570	1335
1953	279	149	236	141	805
1954	161	470	111	438	1160
1955	259	423	190	432	1301
1956	289	349	165	382	1225
1957	267	412	252	398	1349
1958	290	386	151	513	1340
1959	373	150	204	129	922
1960	224	504	176	311	1015
1961	223	138	177	122	660
1962	134	338	103	320	920
1963	208	243	134	220	805
1964	191	7	148	6	352

during a year, it is evident that the number of young birds of the current year's brood must equal the number of older birds that died during the year. The percentage of young birds in the fall population would, therefore, be equal to the mortality rate of the adults for the past year (Burkitt 1926, Farmer 1955). Even with large year-to-year fluctuations in population, if the

population size is the same at the end as at the beginning of a period of years, the total number of young must equal the total number of deaths, and the average mortality rate is given by the sum of the yearly numbers of young as a percentage of the sum of the total population each year. The proportions of young among hunter-killed birds gives the same result.

If hunting methods and intensity do not change on the average over a period of years, as in the Shandon area according to notes kept by McMillan (Personal communication) during the hunting seasons from 1951 to 1962, it is reasonable to assume that any progressive change in population size would be reflected in a parallel change in kill statistics. Year-to-year variations in both population and kill would tend to average out in a few years. The kill on the Shandon area for the 6 years, 1951-1956, totalled 4,279 birds, an average of 713 per year; and for the following 6 years, 1957-1962, 4,294 birds, or 716 per year. No appreciable change in the population is indicated, and the data may, therefore, be used to estimate average survival rates.

Table 4. Contributions to changes in a model population attributable to mortality rates different in females than in males, and to reproductive rates different from the rate required to replace losses. (See text for definitions).

YEAR	ADULT FEMALES			IMMATURES			TOTAL CHANGE IN POPULATION	
	Pr. No.	Calc. No.	Diff.	Repl. No.	Calc. No.	Diff.	Number	Percent
1950	204	173	- 29	577	860	+283	+260	+ 26.0
1951	259	277	+ 18	727	45	-682	-664	- 52.7
1952	120	125	+ 5	314	1083	+769	+738	+123.8
1953	280	230	- 50	770	200	-570	- 530	- 39.7
1954	160	111	- 49	404	565	+161	+335	+ 44.2
1955	242	100	- 142	600	855	+255	+144	+ 12.5
1956	263	163	- 100	752	771	+ 19	- 79	- 6.1
1957	231	252	+ 21	707	810	+103	+124	+ 10.1
1958	275	151	- 124	778	1099	+321	+197	+ 14.9
1959	281	204	- 77	892	285	-607	-624	- 40.4
1960	160	176	+ 16	532	615	+ 83	+ 93	+ 10.1
1961	200	177	- 23	585	260	-325	-354	- 34.9
1962	127	103	- 24	381	604	+223	+259	+ 39.2
1963	182	134	- 48	531	463	- 68	-110	- 12.6
1964	150	148	- 2	461	13	-448	-453	- 50.3

Construction of the model population also requires some assumption as to survival rates. Because the number of adult males is generally greater than the number of adult females (Table 1), it appears that variations in the adult sex ratio are the result of variations in female mortality. The assumption is made that the survival of adult males each year is constant, and equal to the mean survival rate of 0.421 derived from the total numbers of adult and immature males in hunting samples from 1952-1962. The model population is calculated by starting with a cohort of 1,000 birds, and dividing it into sex and age-classes in the same proportion as the observed hunting sample in the initial year. The total number of males is then multiplied by the assumed survival rate to give the number of adult males the following year. The numbers of adult females and immature males and females are then calculated to give the same ratios to adult males as in the hunting sample. This procedure was carried out in successive years to give the model population shown in Table 3.

From this survival table, a further analysis was made to show the contributions of differential female mortality and production of young to the total population change. This analysis is shown in Table 4. The "Potential Number" of females (column 2) is the number that would be present if the survival rate were the same as that assumed for males; the difference (column 4) from the calculated number given in Table 3 (column 3) is the number of females which die in excess of the expected number (negative sign); the three cases with a small positive difference probably represent sampling errors, since differences of about 20 are not significant in a population of the postulated size. The "Replacement Number" of immature birds (column

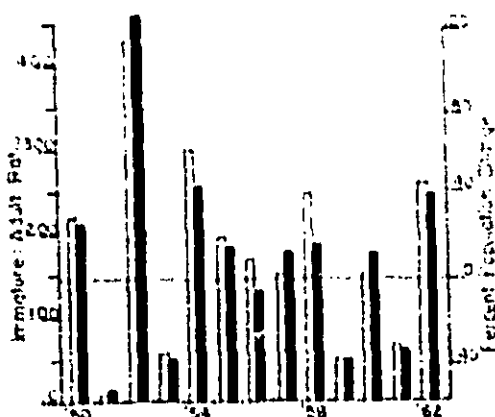


Fig. 1. Population Indexes of California quail populations in the Shandon area, 1950-1962. White bars—ratio of immature to adult birds in fall hunting samples; black bars—percentage change in the model population size.

5) is the number required to maintain the population on the assumption of a constant mortality rate for adults. The estimated numbers calculated in Table 3 are shown in column 6, and the difference from the "Replacement Number" in column 7. The final columns show the total population change in numbers and as a percentage of the previous population. Fig. 1 shows the percentage population change as computed by this method, as well as the immature:adult ratios from the hunting records; the scales have been adjusted to be equivalent.

To test the agreement of the model population with the observed sample, the population totals were summed for the years 1951-1956, and for 1957-1962. In the earlier period, numbers totalled 6,425, and in the latter period 6,412. The model population, therefore, not only has the proportions of the sex and age-classes for each year equal to the proportions in the hunting samples, but also remains at the same level over a period of years, with annual variations superimposed, as do the hunting samples.

The total change in the model population

Table 5. Correlation of hunting-kill statistics with population model parameters.

KILL STATISTICS	POPULATION MODEL PARAMETERS FROM TABLE 4			
	IMMATURE FEMALES	PERCENT CHANGE	"EXCESS" YOUNG	FEMALE SURVIVAL
Imm:Adults	0.983	0.974	0.988	-0.260
Imm:Adult				
Males	0.989	0.993	0.998	-0.123
Imm:Adult				
Females	0.921	0.892	0.922	-0.154

* Ratio of immature birds to potential breeding females (Col. 6/Col. 5).

* Percent annual change in model population (Col. 4).

* "Excess" young produced (Col. 7).

* Percent of adult females surviving (Col. 4).

is due almost entirely to reproduction greater or less than that required to replace losses, and differential female mortality is of minor quantitative importance (Table 4).

Parameters of the model population are correlated ($P < 0.01$) with kill statistics (Table 5). The immature-adult ratio in the fall has, therefore, been taken as the measure of productivity in the populations studied.

Age and Density Factors

Population parameters such as population size, sex ratio, and age ratio may themselves affect productivity and population size. In both the Shandon and Berkeley areas (the only ones with unbroken records), every case of abnormally high reproductive success followed a year in which reproduction was lower than normal. This may have resulted from increased reproduction due to lower population densities; from higher reproductive rates in older females as compared to those in their first breeding season; or from a combination of these effects. Smaller populations, following a year of poor reproduction, have a higher proportion of old birds in the following season's breeding population. Observations of the birds in captivity suggest that the breeding efficiency of older females is more impor-

Table 6. List of independent variables tested for correlation with productivity index.

A.	Proportion of adults among females the previous fall.
B.	Relative size of model population
C.	Total seasonal rainfall through decade 24.
D.	Total rainfall decades 13-21.
E.	Total evapotranspiration decades 13-24.
F.	Total rainfall decades 17-20.
G.	Total evapotranspiration decades 17-20.
H.	Soil moisture (computed) decade 24.
I.	Rainfall amount decade 24.
J.	Accumulated evapotranspiration decade 24.
K.	Rain index decade 20.
L.	Rain index decade 19-21 minus rain index decade 22-24.
M.	Temperature index minus rain index decade 20.
N.	Temperature index minus rain index decades 25-27.
O.	Drought index decades 19-20.
P.	Accumulated temperature above 55 F, decades 19-27.
Q.	Departure of minimum temperature, decades 21-22.
R.	Mean temperature range decades 17-20.
S.	Date of new moon after March 6.

tant than density. In the 2 years in which breeding was observed in Berkeley, with essentially no difference in population density, four adult females hatched 83 chicks in six nests, while three yearling females failed to hatch any chicks at all. There does not appear to be any correlation between reproduction and sex ratio, which was near unity in field data for both 1951 with very poor reproduction, and 1952, with the highest reproduction rate observed (Table 1).

Two population parameters were, therefore, calculated for the Shandon area for use in regression analysis. These were:

- The percentage of adults among females in the preceding fall hunting sample.
- The size of the model population.

WEATHER PARAMETERS

To use weather data meaningfully, parameters bearing a biological relation to the

quail population must be developed from the temperature and precipitation data. Climatic data are used only as an index to the total weather pattern. In order to develop such parameters, the biological effects of various weather conditions on quail, both as reported in the literature, and suggested by field observations in this study, were considered, and working hypotheses formulated as to the possible relations between weather parameters and the subsequent quail reproduction. Development of rainfall parameters are discussed below in some detail, and other factors are treated more briefly.

Rainfall

Both the amount and distribution of rain have been frequently noted to affect the reproductive rate of quail and other birds. In semi-arid regions, low rainfall is associated with reduced reproduction, and above normal rainfall with good reproduction (Grinnell et al. 1918, Gullion 1960, Sows 1960, Calliziot and Welb 1961, Hungerford 1964). Williams (1959:212-215) found that a wet spring delayed the onset of breeding in California quail in New Zealand by 2 weeks. Raftt (1960) found no correlation of precipitation with productivity of California quail, but noted variations in vegetation corresponding to year-to-year differences in rainfall.

The effect of rainfall on quail reproduction may depend on the response of vegetation to rainfall (Summer 1935, Lehmann 1948, MacGregor and Inlay 1951, Hungerford 1964). Similarly, field observations in my study showed good productivity of California quail in 1963, when green vegetation and annual forbs were abundant following high winter and spring rainfall. Poor quail productivity occurred in 1964 when vegetative growth was poor following low rainfall. The drier Shandon area pro-

Table 7. Immature adult quail ratios in three areas, different rainfall.

Area	MEAN RAINFALL	IMMATURE ADULT	
		1963	1964
Berkeley	32.80	2.83	0.17
Hastings	19.33	5.39	0.71
Shandon	9.56	1.35	0.01

duced fewer young than the wetter Berkeley and Hastings areas in both years (Table 7). The hypothesis is suggested that rainfall effect on quail productivity may operate through its effect on vegetation. Nutritional deficiencies (Vitamin A or other yet unidentified factors) and variations in cover are two mechanisms which have been suggested.

Vegetation growth depends on the amount of rainfall, its distribution during the year, and the temperature at the time water is available to the plants. The joint effect of rainfall and temperature on vegetative growth was studied by Thornthwaite (1948) and Thornthwaite and Mather (1955), who developed an empirical formula for "potential evapotranspiration" (Thornthwaite 1948:89-91). Potential evapotranspiration is defined as the amount of water which will be evaporated and transpired under the temperature regime of a given locality with an unlimited water supply. The value is calculated from the temperature data for the locality. The actual (computed) evapotranspiration is determined by a "bookkeeping" method, in which the potential evapotranspiration is compared with the amounts of water available from rainfall and from soil moisture storage (Thornthwaite and Mather 1957, Francis 1967). Although the concept has certain theoretical drawbacks (Pelton et al. 1960), evapotranspiration has proved, for practical purposes, to be an excellent indicator of vegetative growth in California and

elsewhere (Atkley and Ulrich 1962, Atkley 1963, Major 1963).

On the hypothesis that quail reproduction is influenced by vegetative growth, which is controlled by the accumulated evapotranspiration from September to some critical period in the breeding season, I calculated the Thornthwaite evapotranspiration by 10-day periods for each year considered. Preliminary calculations indicated that the evapotranspiration effect was greatest when summed through decade 24 (late April); accumulated evapotranspiration for that period was then selected as the weather parameter with which to test the particular hypothesis.

Similar methods were used to examine other possible effects of rainfall amount and distribution. The weather parameters testing these effects were chosen as follows:

- C. Total seasonal rainfall through decade 24 (late April).
- D. Total rainfall decades 13-21 (January-March).
- E. Total evapotranspiration decades 13-24 (January-April).
- F. Total rainfall decades 17-20 (mid-February-mid-March).
- G. Total evapotranspiration decades 17-20 (mid-February-mid-March).
- H. Computed available soil moisture decade 24 (late April).
- I. Rainfall amount in decade 24 (late April).
- J. Accumulated evapotranspiration through decade 24 (late April).

Rain may also act as a trigger or a deterrent to breeding if it occurs at a critical time, without regard to the total amount except in a broad sense. Lehmann (1946: 112) noted that breeding was resumed by Texas bobwhites when summer rains occurred, but that during incubation, birds left their nests at the first sign of a shower.

Drought, or the continued non-occurrence of rain, has often been cited as an inhibitor of breeding (for example, Errington 1945: 14, Lehmann 1953:221); Nee (1937:210) noted that drought has an indirect effect via the food supply. Marshall (1959:463) found rainfall to be a powerful regulator of breeding in birds, especially in arid regions. "Bad weather," which in context usually refers to a combination of rain and low temperatures, has been frequently mentioned as a cause of delayed breeding or reduced productivity. Lewin (1963:259) found earlier breeding in California quail when a rainy March was followed by a dry April than in the reverse situation. Low temperatures in conjunction with rainy days have been related to population levels; Allison (1962), using paired factors of temperature and precipitation, found New England grouse (*Bonasa umbellus*) populations fluctuate with degree-days above 65 F, and with the total rainfall for the last 2 weeks of May.

The effects of the occurrence or non-occurrence of rain, with or without accompanying cold, were tested by the use of the following weather parameters:

- K. Rain index at decade 20 (mid-March).
- L. Sum of rain indices for decades 19-21 (March) less the sum of rain indices for decades 22-24 (April).
- M. Temperature index minus rain index for decade 20 (mid-March).
- N. Temperature index minus rain index for decades 25-27 (May).
- O. Drought index for decades 18-20 (early February to mid-March).

Temperature

Quail may be killed directly by cold (Grinnell et al. 1918, Kendeigh and Baldwin 1937) or by exposure to the heat of the sun (Summer 1935). Hatchability of eggs may

be affected by temperature (Hickey 1955, Landy 1962, Romanoff 1934, Yeatter 1950). Timing of the breeding cycle and variations in reproductive physiology and behavior are related to temperature (Nicc 1937, Lehmann 1946, Marshall 1949, 1959:467; Marshall and Coombs 1957, Buss and Swanson 1950, Lewin 1963, Crawford 1962, Somes 1962).

Field observations in this study do not provide any evidence of mortality due to extreme temperature, or of temperature effects on eggs. In fact, very little mortality from any cause was noted, the few cases being caused by accident or predation. Fertility and hatchability of 95 eggs found and tested was 92 percent, with no difference between 1963 and 1964. Temperature may have affected the time of onset of breeding behavior, with some effect on productivity; and temperature during the breeding season may have affected the vigor of the laying hen and indirectly the viability of the chicks.

Weather parameters selected to test temperature effects were as follows:

- P. Accumulated temperature excess above 55 F for decades 19-27 (March, April, May).
- Q. Departure of minimum temperature from the mean of the two preceding years, for decades 21-22 (late March-early April).

Light

The photoperiod, or length of day, is an important factor controlling the onset of reproductive activity of birds (Rowan 1925, 1926, 1938; Burger 1949). While the astronomical day length on a given date does not vary from year to year, it is evident that in nature there must be a threshold of light intensity that delimits the end of the light period, and a threshold that delimits the end of the dark period. Threshold intensities may be reached at different times with

respect to astronomical sunrise and sunset (Sumner 1935, Davis 1955, Emlen 1937, Leopold and Eynon 1961, Shaver and Walker 1931). The variations are related to cloudy versus clear skies, and to the brightness of moonlight. The few days immediately following the full moon have a small increment of light in the early morning that, in effect, produces an earlier daybreak and a longer length of day. The total variation may be as much as 40 minutes between a cloudy and a clear day (Bartholomew 1949:465). Such differences in effective day length are equivalent to several weeks advance or delay in the season, and may affect the reproductive success.

Cloudy days are characterized by lower maximum temperatures, as a result of reduced solar radiation reaching the surface during the day, and by higher minimum temperatures from reduced net outgoing radiation from the surface during the night. The daily range of temperature, the difference between the maximum and the minimum, is closely correlated with the duration of cloudy weather. Light effects on reproduction may thus be tested by cloudiness, expressed in terms of daily temperature range, and by the moon phase, expressed as the date of full moon. The parameters selected were the following:

- R. Mean temperature range (maximum minus minimum) for decades 17-20 (mid-February-mid-March).
- S. Number of days after March 6 that full moon occurs.

Table 6 lists the independent variables used in the regression analysis which may be causative factors in quail population changes.

STATISTICAL ANALYSIS

The relationship between the juvenile: adult ratios (Y) in the Shandon area (Table

1) and the variables shown in Table 6 was analyzed by a stepwise multiple linear regression, using an IBM 1620 computer with a program written by Boles (1963). At each step, coefficients for the multiple regression equation, the standard error of Y on X , the squared correlation coefficient, the sum of the squares of the residuals, the standard error of each coefficient, and the t -ratio for each coefficient were computed.

Simple Correlation

High correlations ($P < 0.01$) were found between the juvenile:adult ratio and the following variables:

- A. Proportion of adults among females the previous fall.
- B. Relative size of model population.
- C. Total seasonal rainfall through April.
- D. Total rainfall January-March.
- E. Total evapotranspiration January-April.
- H. Soil moisture (computed) late April.
- J. Accumulated evapotranspiration late April.
- M. Temperature index minus rain index mid-March.

Some correlations were found which statistically would appear to be significant but cannot logically have any causal connection. For example, the percent of adult females in the preceding fall sample is significantly correlated ($P < 0.01$) with the occurrence of rain in the middle of March ($r = 0.677$). High correlation ($P < 0.01$) is also found between the date of the new moon (S), and both mean temperature range in decades 17-20 (R) and the occurrence of rain and low temperature in mid-March (M). Although the first inclination is to dismiss these as spurious or accidental, there is a possibility that there may be a real, if undefined, relationship. Brier and Bradley (1964:387-388) have shown a sig-

nificant ($P < 0.001$) cycle of 14.765 days in precipitation data for the United States, equal to exactly one half of a lunar month, and they suggest that the causal factor is lunar. Land (1965) found a lunar period in sunshine observations in the United States, and Siivonen and Koskimies (1955) have shown population fluctuations in phase with the lunar cycle.

Multiple Regression Analysis

In view of the correlation existing between most of the weather variables being considered, only a limited amount of information can be gained from the above simple correlations. Multiple linear regression of the juvenile:adult ratio (Y) on the 19 variables of Table 6 (17 weather parameters and two population parameters) for the years 1949-1962 yielded the following regression equation for the quail reproductive index in this area:

$$Y = 0.029 H + 0.021 A - 0.120 C - 0.975, \\ R^2 = 0.988$$

All of the coefficients in the above equation are significantly different from zero ($P < 0.01$). The goodness of fit to the observed value of Y is measured by the squared correlation coefficient R^2 , which is equal to 1 - (the ratio of the residual variance to the total variance of the dependent variable Y).

The quantitative importance of the additional variable added in each step is indicated by the amount by which R^2 is increased and the residual variance is decreased. With the single variable H (soil moisture), $R^2 = 0.831$; addition of variable A (proportion of adults among females) increases R^2 by 0.124; variable C (seasonal rainfall) by 0.033.

In brief, the variance of the productivity index Y is due to all three factors which account for almost 99 percent of the variance

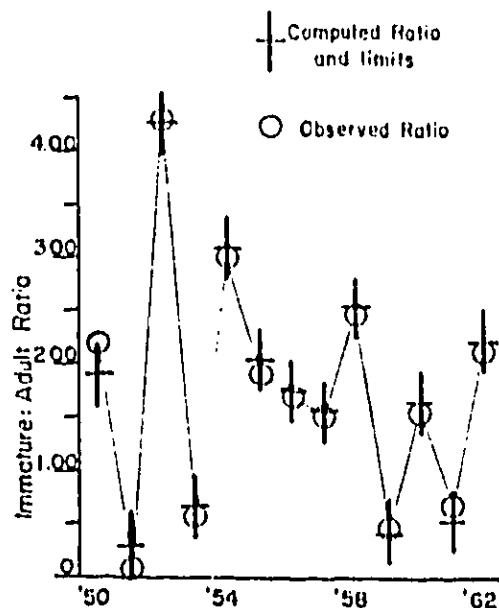


Fig. 2. Observed ratios of immature to adult birds in fall hunting samples in the Shandong area and ratios calculated from the regression equation $Y = 0.929 H + 0.021 A - 0.120 C - 0.975$. Data from hunting records for the period 1950-1962.

of the reproductive index. A fourth variable, seasonal evapotranspiration to the end of April, contributes very little more, reducing the variance by less than 1 percent.

The closeness of fit of the values of Y calculated from the above equation, indicated by the R^2 value of 0.988, is illustrated in Fig. 2, in which the vertical bars represent the calculated values plus or minus two standard errors, and the observed values are indicated by circles. The fit is striking, since only three independent variables have been used in this case to calculate the 13 points.

Details on the methods of calculation and the results of tests on independent data have been previously reported (Francis 1937). The close agreement found between observed indices of reproductive success and those computed from independent data

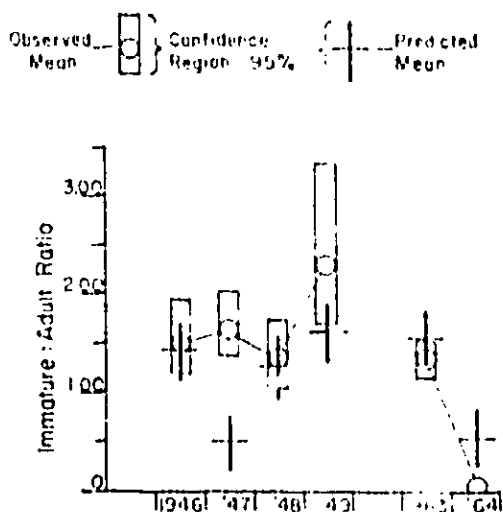


Fig. 3. Ratio of immature to adult quail predicted from independent data by the regression equation $Y = 0.929 H + 0.021 A - 0.120 C - 0.975$, and observed ratios in the hunting samples for 6 years.

(Fig. 3) is convincing evidence that the factors in the above regression equations determine population levels in the Shandong area for all but a few exceptional years.

The apparent discrepancy for 1964 is attributed to the observed ratio being nearly zero. In this case, confidence limits could not be computed, and it is also reasonable to expect departure from linearity. The 1947 discrepancy remains unexplained. The incomplete data for this year required that the proportions of adults among females be estimated, and the estimate may have been in error.

DISCUSSION

The mechanisms by which these weather factors affect quail reproduction can only be conjectured. Direct observations of both captive and wild birds suggest that a proximate factor is the behavior of the birds during the breeding season. Differences were very noticeable in pair formation, incubation

tion behavior, and care of the young, between the 2 years of the study. In the clutches which were successfully hatched in the enclosure at Berkeley, survival of the young made the difference between the 2 years. Parental care appeared from my observations, to be responsible for the greater survival in 1963, but neither viability of the chicks due to an influence of earlier conditions on the parents' physiology, or a more direct influence of the quality of food available to the chicks, can be ruled out.

Evidence that the differences in reproduction in the Shandon area were related to hormone levels is given by the gonadal development of specimens. Of nine specimens examined in 1963, eight were in breeding condition, while in 1964 only one of six was in possible breeding condition in early June ($P < 0.05$). Early molt gives stronger evidence, with all of 57 trapped birds molting on June 8.

The effect of Vitamin A remains obscure. Hungerford (1964) related quail productivity to vitamin A storage in the liver in Gambel quail. His June specimens showed lower vitamin A levels in a year of good production of young, while specimens in my study had relatively high vitamin A levels in June when almost no young were produced. In view of the rapid change in vitamin A storage that occurs after precipitation (Hungerford 1964:145), my data cannot be compared with his for other months.

It seems likely that differences in reproductive success are related to the plant species which are abundant under the different rainfall regimes, and to the time of year when they are growing most vigorously and have a high nutritive value. Observations in the present study, both in the field and in the enclosure, showed striking differences in the vegetation composition, years of good

quail reproduction being those with an abundance of annual forbs, including legumes, known to be important as quail foods. Species of plants and growth stage may be more important to quail nutritionally than the production of food in quantity.

As a working hypothesis, it appears that the temperature and rainfall regime in a given year is responsible for the production, prior to the beginning of the quail breeding season, of highly nutritious plant foods which, under optimum conditions, supply all the elements (protein, vitamins, and other) necessary for vigorous reproductive behavior. An appropriate photoperiod will trigger the beginning of the reproductive season; if nutrients are present in an adequate amount, gonadotropic secretions of the pituitary will lead to full gonadal development, as evidenced by pairing, aggressive behavior, vocalizations, mating, etc., followed by nesting and egg-laying. Normal environmental stimuli, and perhaps gonadal feed-back to the pituitary, will then stimulate the production of prolactin and other hormones associated with incubation and with parental behavior; such hormones are more readily elicited in experienced females than in those breeding for the first time. With deficiencies of essential nutrients, the pituitary will produce subnormal amounts of both gonadotropins and prolactin, and both reproductive and parental behavior will be expressed at a low level, resulting in poor hatches of eggs and poor survival of young.

There remains a wide field of inquiry in many aspects of the system here postulated. It would be desirable to determine the variations in species, and in the timing of growth of plants under different weather conditions; the nutrient value of both seeds and vegetative parts of these plants; the levels of vitamins and other nutrients in quail feeding on particular plants; the de-

velopment of the gonads and the accompanying reproductive behavior; the normal changes in vitamin levels and in endocrine production at each stage of the breeding cycle, and their variation with weather conditions; and the complex neuroendocrine relations involved in behavior at all stages of the reproductive cycle.

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Received for publication April 11, 1969.